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Management and Conservation Article

Barred Owl Space Use and Habitat Selection in the Eastern Cascades, Washington

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ABSTRACT Competition with barred owls (*Strix varia varia*) is an important factor contributing to the continued decline of threatened northern spotted owl (*Strix occidentalis caurina*) populations in the Pacific Northwest, USA, but basic information on habitat selection and space use patterns of barred owls is lacking for much of the region. We investigated space use and habitat selection by tracking radiotagged barred owls in the Eastern Cascade Range of Washington, USA, from 2004 to 2006. We surveyed for barred owls across the 309-km^2 study area and confirmed presence of barred owl pairs at 21 sites. We collected movement data on 14 barred owls from 12 sites. Mean annual 95% fixed-kernel home-range size was 194 ha for females ($n = 4$, SD = 70) and 288 ha for males ($n = 5$, SD = 114). Home ranges were located more frequently than expected in areas with low topographic position, gentle slopes, large overstory tree-crown diameter, high normalized difference vegetation index (NDVI), overstory tree canopy closure >72%, and a moderate amount of solar insolation. Within home ranges, areas that had large tree-crown diameters, low topographic positions, and gentle slopes were used more frequently than expected. The resource selection function we developed for barred owls in our study area indicated that barred owls used areas with the combination of low values for topographic position and slope and higher values for NDVI, solar insolation, and an interaction term for canopy closure and tree-crown diameter. In comparison to published information on northern spotted owls, barred owls used areas with similar canopy closure and tree size classes, but barred owl home ranges were much smaller and more concentrated on gentler slopes in valley bottoms. This information may contribute to the development of management practices that maintain forest characteristics appropriate for spotted owl habitat and prey in areas where spotted owls are least likely to be excluded by territorial barred owls in the Eastern Cascades of Washington.

KEY WORDS barred owl, habitat selection, home range, northern spotted owl, *Strix occidentalis*, *Strix varia*, Washington.

Competition with barred owls (*Strix varia varia*) is an important factor contributing to the decline of northern spotted owl (*Strix occidentalis caurina*) populations, but the specific ecological mechanisms underlying interactions between these species are poorly understood (Courtney et al. 2004, U.S. Fish and Wildlife Service 2008). The distribution of barred owls has expanded from their historic range within the deciduous forests of eastern North America into western coniferous forests during the recent past (Mazur and James 2000). Barred owls were first recorded in Washington and Oregon, USA, in the 1970s (Taylor and Forsman 1976). They now occur throughout the range of the northern spotted owl and much of the range of the California spotted owl (*Strix occidentalis occidentalis*) and are relatively common in parts of their recently occupied range (Steger et al. 2006). During the same period, spotted owl populations have declined, particularly in the northern portion of their range where barred owls are most abundant (Anthony et al. 2006). These declines have occurred despite implementation of habitat protection under the Northwest Forest Plan (Lint 2005).

Like spotted owls, barred owls are associated with interior forests (Mazur and James 2000). As sit-and-wait predators, both spotted and barred owls need trees large enough to provide adequate roosts, stands that have appropriate tree spacing to provide good flight opportunities, and understory characteristics that enhance prey vulnerability (Courtney et al. 2004, Livezey 2007). Potential effects of expanding barred owl populations on spotted owls include displacement (Kelly et al. 2003, Olson et al. 2005), competition for prey (Hamer et al. 2001), and hybridization (Haig et al. 2004, Kelly and Forsman 2004). However, barred owls are not the only threat to spotted owls. Other threats include habitat loss from large-scale, high-intensity wildfires; persistent infestations of defoliating insects; and forest management practices, including timber harvests and fuel-reduction treatments (Courtney et al. 2004, Lint 2005, U.S. Fish and Wildlife Service 2008). Understanding how the presence of barred owls interacts with other threats to spotted owls is important for developing and implementing effective conservation strategies for spotted owls and for integrating spotted owl conservation with other forest management objectives (Gutierrez et al. 2007, Lehmkuhl et al. 2007, Livezey and Flemming 2007, U.S. Fish and Wildlife Service 2008).

Although many aspects of spotted owl ecology have been well studied (Courtney et al. 2004), information on barred owl ecology in areas where they are sympatric with spotted owls is limited (Gutierrez et al. 2007, Livezey and Flemming 2007). To our knowledge only one radiotelemetry study on barred owl ecology in the Pacific Northwest has been published, to our knowledge (Hamer et al. 2001,

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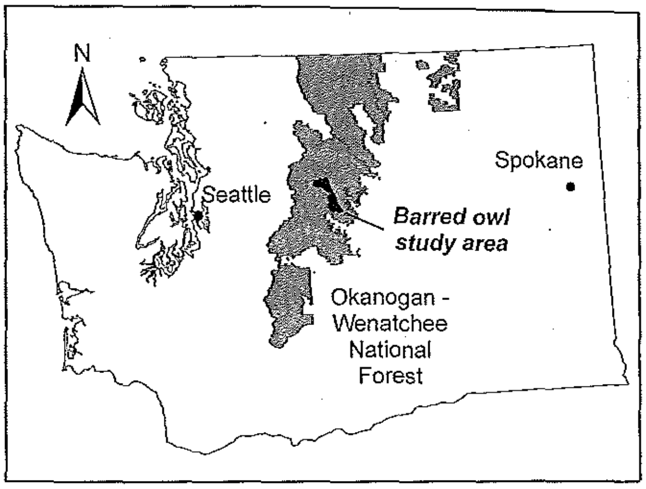

Figure 1. Map of the area where barred owls were surveyed and radiotracked in the Eastern Cascade Mountains, Washington, USA, from March 2004 to September 2006.

2007). Most of the current knowledge of barred owl ecology in the Pacific Northwest has been drawn from information collected incidental to spotted owl management and research (Livezey and Flemming 2007).

Our objectives were to 1) quantify space–use patterns of barred owls, 2) identify factors that were important determinants of whether a habitat was selected by barred owls, and 3) model the relationship between those factors and the relative probability of habitat use by barred owls. Our goal was to provide information on habitat selection by barred owls that could be compared with existing information on northern spotted owls to contribute to conservation and recovery planning for spotted owls.

STUDY AREA

Our study area encompassed 309 km^2 in the interior, mixed-conifer vegetation zone near Leavenworth and Lake Wenatchee in Chelan County, Washington, USA (120°35′W, 47°48′N; Johnson and O'Neil 2001; Fig. 1). The study area was composed primarily of lands within the Wenatchee River Ranger District of the Okanogan–Wenatchee National Forest (81% of the study area). Other land ownership included Washington Department of Natural Resources, commercial timber lands, and other private land owners. The elevation within the study area ranged from 500 m to 1,900 m.

We chose this area because it provided an opportunity to investigate barred owl habitat use across a range of environmental conditions associated with the steep precipitation gradient found on the east side of the Cascade Range. Average annual precipitation across the study area ranged from 150 cm at the northwest edge to 50 cm at the southeast edge. Forests in the northwestern portion of the study area were predominantly in moist grand fir (*Abies grandis*) series plant associations, with Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*) as common overstory species (Lillybridge et al. 1995). The southeastern portion of the study area (farthest from the Cascade Crest) supported dry grand fir and Douglas-fir series plant associations, with northern exposures having an overstory of Douglas-fir and southern exposures having open ponderosa pine (*Pinus ponderosa*) or nonforest cover types (Lillybridge et al. 1995). This was a fire-prone landscape where integrating measures for conservation of spotted owl habitat and fire-risk reduction was problematic, and potential interactions between barred and spotted owls complicate management.

Spotted owls were surveyed systematically in the area from 1989 to 2002, with some records dating back to 1981 (Irwin et al. 2004; W. Gaines, United States Forest Service, Okanogan–Wenatchee National Forest, unpublished data). This area was within the Wenatchee spotted owl demography study area (Anthony et al. 2006). From 1991 to 2004, 17 spotted owl sites were documented, with a maximum of 9 sites confirmed to be occupied by pairs during any single year (Irwin et al. 2004; W. Gaines, unpublished data). Incidental detections of barred owl were recorded during spotted owl surveys, although no follow-up visits were conducted to document barred owl sites or determine pair status. The first detection of barred owls in the study area was in 1981, the first year of any spotted owl surveys. Barred owls have been recorded in the area nearly every year since.

METHODS

Field Methods

We used broadcast calls to survey barred owls during the breeding season to locate territorial pairs. Our methods for surveying and for determining the status of sites were consistent with those used for spotted owls (Lint et al. 1999), with minor modifications to focus on barred owls. We located call-survey stations approximately 1 km apart in forested portions of the study area (n = 160 stations) and attempted to visit each station 3 times between 1 March and 31 August each year. We played barred owl 8-note location and agitated calls for 20 minutes at each station. We also played spotted owl calls to survey 16 stations that surrounded 4 spotted owl sites within the study area where occupancy of spotted owls had been documented since 1999. We did not survey the entire study area for spotted owls.

After confirming the presence of a pair of barred owls, we attempted to capture both owls at the site. We did not attempt to capture unpaired owls. We lured barred owls into mist nets using mice or simulated territorial interactions (Elody and Sloan 1984). After capture, we recorded weight and basic body measurements. We determined sex, based on behavior, vocalizations, weight, measurements, or presence of a brood patch (Carpenter 1992). We radiotagged captured owls with backpack-mounted Holohil RC-9 transmitters (9–11 g; Holohil Inc, Woodlawn, ON, Canada). We used tail-mounted radiotransmitters (Reid et al. 1996) in spring 2004, but thereafter used backpack-mounted transmitters (Guetterman and Burns 1991) after poor retention of tail-mounts on 5 individuals early in the study.

We used standard radiotelemetry triangulation methods to locate owls (Guetterman and Burns 1991, Kenward 2001).

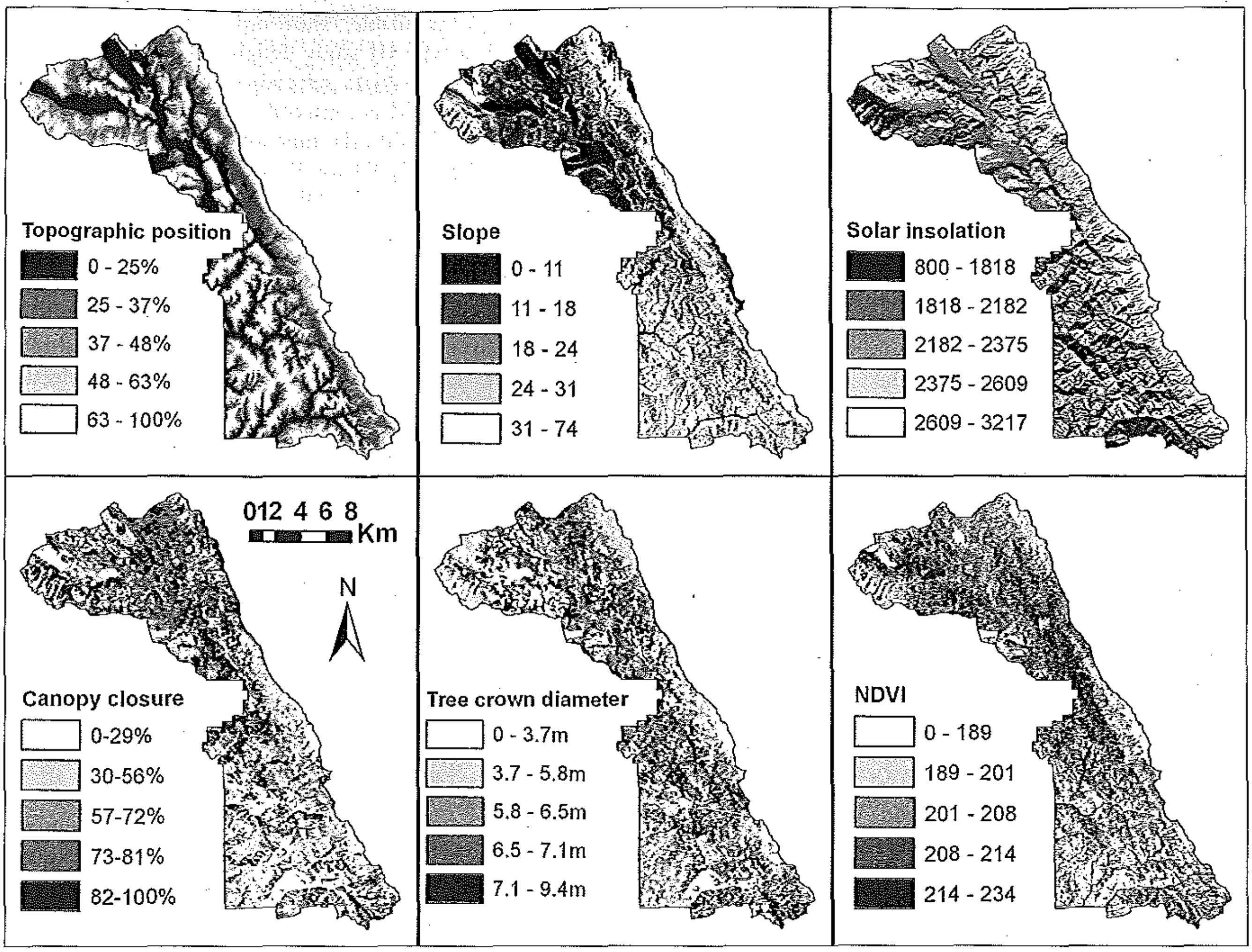

Figure 2. Maps of habitat characteristics used to evaluate resource selection by barred owls in the Eastern Cascade Mountains, Washington, USA, based on data collected from 2004 to 2006. Habitat characteristics are 1) topographic position, 2) slope, 3) solar radiation, 4) canopy closure, 5) overstory tree crown diameter, and 6) normalized difference vegetation index (NDVI).

We documented locations of tagged owls ≥ 2 times per week, with a minimum of 24 hours between locations to minimize autocorrelation (Swihart and Slade 1997). We tested telemetry location accuracy in the field by placing a transmitter at a known location (determined by handheld Global Positioning System units) within the home range of a radiotagged barred owl and having a naïve observer triangulate the location of the transmitter using standard field procedures.

Our goal was to collect ≥ 50 locations per season for each tagged owl (Seaman et al. 1999). We excluded seasonal subsets of data from home-range and habitat-selection analysis if an owl had <30 locations during that season, with the exception of one male with 28 locations during the only season it or any other owl was radiomarked at that site. We included that individual in the analysis because it was using a relatively dry area that was important to represent in the analysis. We did not include locations of females on nests in the analysis. We used LOAS software (version 2.12; Ecological Software Solutions, Hegymagas, Hungary) to check field estimates of triangulated locations and screen for errors. We calculated seasonal and annual minimum convex polygon (MCP) and fixed-kernel home ranges (KHR) with individual least-squares cross-validation to determine bandwidth with the Animal Movement ArcView extension (Hooge and Eichenlaub 1997).

Spatial Data

We compiled maps of stand-scale vegetation and topographic characteristics for the study area using a Geographic Information System (GIS; ArcGIS version 9.2; Fig. 2). We resampled all GIS data to 20-m grid-cell resolution for analysis. We derived slope, topographic position, and solar insolation from a United States Geological Survey 10-m digital-elevation model and calculated slope in degrees using ArcGIS spatial analyst. We calculated topographic position as the percentile of the focal cell in the elevation range within a 1-km radius of that cell (elevation at the cell minus the min. elevation within 1 km, divided by the elevation range [the max. elevation minus the min. elevation] within 1 km). Low values correspond to valley bottoms and high values to ridge tops. We calculated solar insolation using the ArcGIS solar analyst extension. Solar insolation quantifies the amount and intensity of direct sunlight at a pixel, based on aspect, slope, surrounding topography, and atmospheric transmission based on latitude. The ArcGIS solar insolation calculation does not correct for cloud cover or other weather factors. The unit of measurement for solar insolation is annual mean daily watt–hours of solar energy per square meter.

We used object-based classification techniques (Blaschke et al. 2006) to develop stand-scale maps of overstory tree canopy closure and dominant overstory tree-crown diameter from a 60-cm-cell resolution QuickBird satellite image (Digital Globe, Longmont, CO) taken in August 2006. Object-based image classification derives polygon maps of forest-stand characteristics by mimicking the reasoning used by human image interpreters, including size, shape, and texture of patches, in addition to the spectral characteristics used in conventional pixel-based image classification (Campbell 2007). We conducted the classification in 4 steps: 1) unsupervised polygon delineation using E-Cognition pattern recognition software (Definiens Imaging, Munich, Germany); 2) interactive attribution of a training sample of polygons (n = 2,489, 17% of the polygons) with cover type (water, forest, nonforest, road), canopy closure, and dominant overstory tree-crown diameter determined by on-screen interpretation; 3) classification tree and regression modeling to predict cover type, canopy cover, and crown diameter based on polygon spectral and textural characteristics; and 4) field sampling to determine map accuracy. Overall map accuracy based on 13 cover and structure types sampled at 64 test plots was 83%, with 94% of plots within one canopy or crown-diameter class. We also calculated normalized difference vegetation index (NDVI) from the QuickBird satellite image using ERDAS Imagine (version 9.1; Leica Geosystems Geospatial Imaging, Saint Gallen, Switzerland).

Statistical Analysis

We conducted our statistical analysis in 2 steps. First, we calculated univariate selection ratios (S) for each habitat characteristic at home range (second order) and within home range (third order) scales to identify factors that were important determinants of habitat selection and to investigate the scale at which habitat selection occurred (Johnson 1980, Manly et al. 2002). Second, we developed a resource-selection function to model the relationship between important factors and the relative probability of habitat use by barred owls using mixed-effects logistic regression (Pinheiro and Bates 2000). These 2 analysis approaches provide complementary perspectives on habitat-selection patterns, with the selection ratios providing information on the level of use relative to different classes of the habitat characteristics and the resource-selection function providing a framework for modeling the relationship between the combination of habitat characteristics and relative probability of use.

For the selection ratio analysis, we compared 95% fixed-kernel seasonal home ranges (used) to the study area (available, second-order selection [Johnson 1980], with a type II study design [Manly et al. 2002]), and we compared radiotelemetry locations (used) to 95% fixed-kernel seasonal home ranges (available, third-order selection [Johnson 1980], with a type III study design [Manly et al. 2002]). We calculated univariate selection ratios and Bonferroni-corrected 95% confidence intervals (Manly et al. 2002) using the widesII and widesIII functions from the adehabitat package (Calenge 2007) for R (version 2.6.2; R Development Core Team 2008). We derived habitat classes for categorical univariate analysis from continuous GIS variables by dividing the study area into 5 equal area classes (Fig. 2). We compared third-order selection ratios between sexes, between seasons, and between time periods (i.e., midday, morning, evening, and night) to evaluate whether there were important differences in habitat selection associated with these factors.

We estimated a population-level resource-selection function using a mixed-effects logistic regression model. We used the lmer function (family = binomial) from the lme4 package in R for our analysis. We compared telemetry locations (used, n = 1,578) to the same number of random points drawn from the study area (available) in a type II study design (Manly et al. 2002). We examined a correlation matrix for all covariates before modeling to screen for collinearity. Using logistic regression with use–availability data presents some problems because predicted values are not scaled between 0 and 1 and generally do not reflect true probabilities of resource selection (Manly et al. 2002, Keating and Cherry 2004), but logistic regression can provide an informative and unbiased method for ranking habitat use and for comparing relative probability of use (Keating and Cherry 2004, Johnson et al. 2006). We used individual owls as a random-intercept effect in our mixed-effects logistic regression analysis to address issues associated with autocorrelation and uneven sample sizes between individuals (Pinheiro and Bates 2000, Gillies et al. 2006). We analyzed all biologically realistic combinations of covariates shown to be related to barred owl habitat use in the selection ratio analysis. We also evaluated a quadratic form for solar insolation (including solar insolation and solar insolation-squared) and an interaction term for canopy closure and tree-crown diameter. We included canopy closure and tree-crown diameter as main effects in all models with the interaction term. We excluded distance to water from the logistic regression analysis based on the results of the selection ratio analysis. We ranked models using Akaike's Information Criterion for model selection (Burnham and Anderson 2002).

RESULTS

We identified 21 unique sites inhabited by pairs of barred owls and 2 sites inhabited by pairs of spotted owls during call surveys from 2004 to 2006 (Table 1). In 2004, we did not complete the full set of surveys across the entire study area, although all stations received $\geq$1 visit. We completed 3 visits per station across the study area in 2005 and 2006. We captured and collected radiotelemetry movement data on 17 barred owls (8 F, 9 M) at 12 sites. Locations during the breeding season (1 Mar–31 Sep) were distributed between midday (0800–1600 hr; 37% of locations), morning

Table 1. Results of surveys for barred owls and the number and characteristics of radiotagged owls by season and year. Survey results indicate the number of sites occupied by pairs, the number of those pairs with young, and the number of sites occupied by resident single owls. The number radiotagged indicates the total number of radiotagged owls, the number of females and males with >30 locations, and the number of sites with pairs where ≥1 individual had >30 locations. Breeding season (BR) was from 1 March to 31 September, and nonbreeding season (NB) was from 1 October to 28 February.

		Survey results			No. radiotagged			
Season	Yr	Pairs	Pairs with young	Resident singles	Total	F ($n > 30$)	M ($n > 30$)	Sites
BR	2004	5	2	4	7	1	3	3
NB	2004				8	2	3	3
BR	2005	18	4	6	15	4	7	11
NB	2005				7	4	3	7
BR	2006	19	10	3	8	1	5	5

and evening (0400–0800 hr and 1600–2000 hr; 35%), and night (2000–0400 hr; 29%). We generally collected locations during the nonbreeding season (1 Oct–28 Feb) during midday (0800–1600 hr; 87% of locations) because of safety considerations associated with winter access to the sites. Median telemetry error from field accuracy tests was 99 m ($\bar{x}$ = 110 m, SD = 76 m, n = 60 test locations). Fourteen radiotagged barred owls (6 F, 8 M) were included in the home-range and habitat-use analysis. Two radiotagged owls were unpaired, nonterritorial individuals, and one female had locations collected only near the nest site. We excluded these 3 individuals from the analysis. Mean annual 95% KHR size was 194 ha (SD = 70, n = 4) for females and 288 ha (SD = 114, n = 5) for males (Table 2). We only had one pair where both individuals were radiotagged for the same 2 consecutive seasons. Annual home-range size for this pair was 332 ha for the 95% KHR and 637 ha for the MCP.

Areas used by barred owls within home ranges differed from availability for all the habitat characteristics we analyzed ($P \leq 0.05$ for second-order selection, based on selection ratios; Fig. 3). Topographic position and slope showed the strongest patterns of selection, with the lowest topographic position (S = 2.41, 95% CI = 2.00–2.87 for topographic position <25%) and the gentlest slopes (S = 2.03, 95% CI = 1.33–2.74 for slope <11°) being used in proportions more than twice their availability. Other attributes that were used more than they were available were the densest canopy-closure classes (S = 1.73, 95% CI = 1.42–2.04 for canopy closures of 72–81%; S = 1.60, 95% CI = 1.04–2.16 for canopy closures of 81–100%), the largest crown-diameter classes (S = 1.47, 95% CI = 1.29–1.65 for crown diam of 7.1–9.4 m; S = 1.52, 95% CI = 1.33–1.72 for crown diam of 6.5–7.1 m), the highest NDVI classes (S = 1.44, 95% CI = 1.02–1.86 for NDVI of 214–234; S = 1.47, 95% CI = 1.35–1.59 for NDVI of 208–214), and areas with moderate solar insolation (S = 1.76, 95% CI = 1.12–2.34 for 2,182–2,375 yr-round daily mean solar energy watt–hr/m^2). For all distance to water classes, confidence intervals overlapped 1, indicating that use did not differ from availability. Although overall use of the landscape in relation to distance to water was different from availability at this scale ($P < 0.01$), no distance to water class was selected or avoided in the placement of the home ranges within the study area.

At the third-order scale of analysis, overall use of canopy closure, crown diameter, topographic position, slope, and solar insolation classes at used locations differed from availability within home ranges, but differences were relatively small compared with the second-order analysis. The strongest patterns of selection within home ranges were avoidance of the lowest NDVI class (S = 0.55, 95% CI = 0.36–0.75 for NDVI <189), the highest topographic position classes (S = 0.52, 95% CI = 0.19–0.86 for topographic position >63%; S = 0.63, 95% CI = 0.50–0.77 for topographic positions of 48–63%), the steepest slope classes (S = 0.46, 95% CI = 0.14–0.78 for slopes >31°; S = 0.74, 95% CI = 0.54–0.94 for slopes 24–31°; S = 0.85, 95% CI = 0.75–0.94 for slopes 18–24°), and the smallest crown-diameter class (S = 0.49, 95% CI = 0.17–0.81 for crown diam <3.7 m). The only classes selected within home ranges were the largest crown-diameter class (S = 1.21, 95% CI = 1.05–1.37 for crown diam >7.1 m), the lowest topographic position class (S = 1.18, 95% CI = 1.09–1.26 for topographic positions <25%), and the gentlest slope class (S = 1.17, 95% CI = 1.04–1.30 for slopes <11°). Although overall use of the home range relative to canopy closure was different from availability ($P < 0.01$), the 95% CI overlapped zero for all canopy-cover classes reflecting the fact that areas within home ranges were predominantly in closed-canopy forests. Overall use did not differ from availability within the home range in relation to distance from water or NDVI. Selection ratios did not differ between sexes, seasons, or times of day (the 95% CI overlapped for all estimates of S).

Table 2. Mean, standard deviation, and sample sizes for minimum convex polygon (MCP) and fixed kernel home-range (KHR) sizes (ha) by sex and season for barred owls in the Eastern Cascade Range, Washington, USA, from March 2004 to September 2006. The 50% KHR home ranges were not calculated for annual home ranges.

		100% MCP		95% KHR		50% KHR		
Season	Sex	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	n
Breeding	F	202	35	195	33	30	20	5
	M	183	67	173	62	24	12	8
Nonbreeding	F	322	253	329	152	49	38	5
	M	429	190	421	227	58	31	5
Annual	F	416	250	194	70			4
	M	477	194	288	114			5

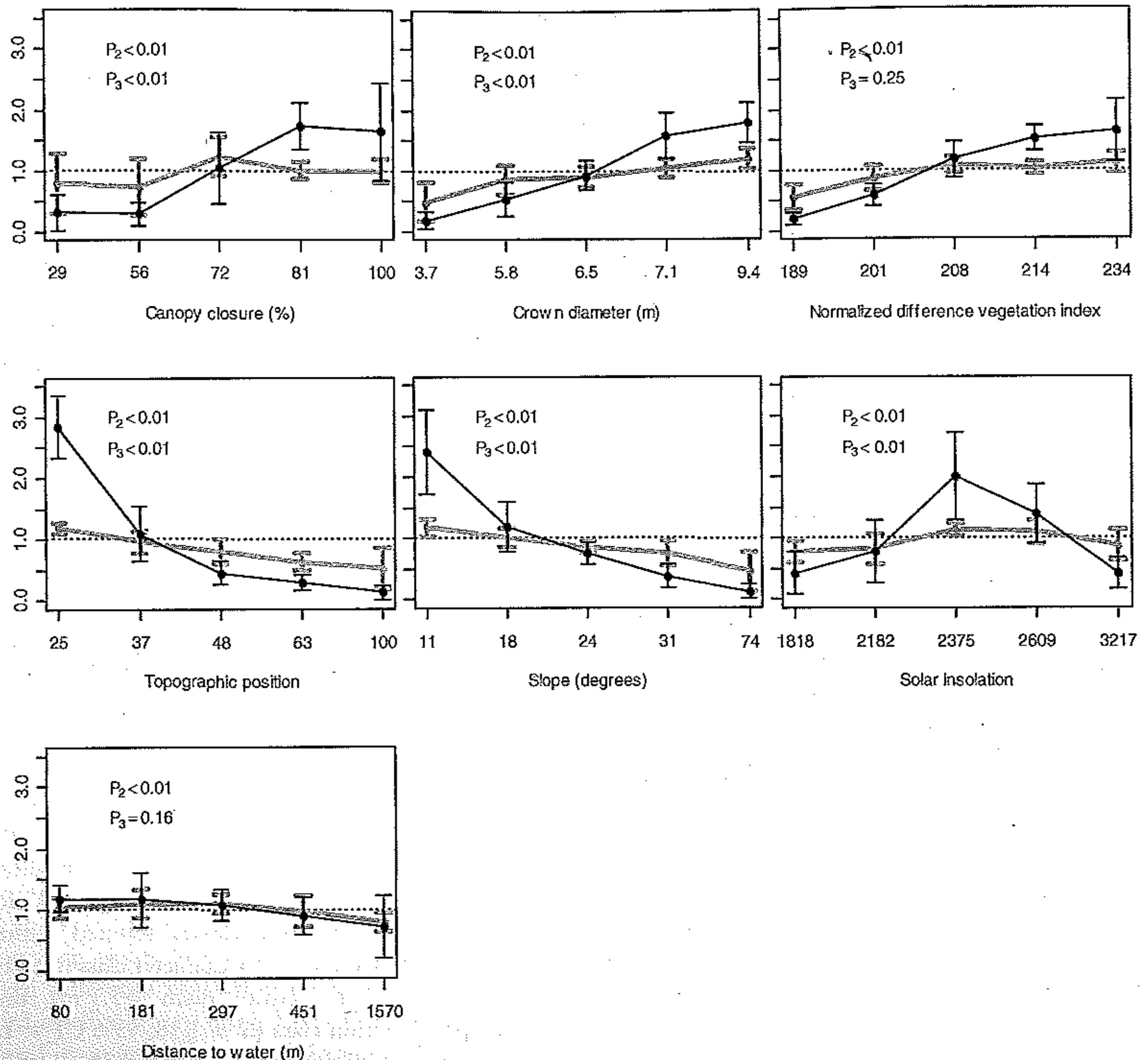

Figure 3. Selection ratios at 2 scales for habitat characteristics used by radiotagged barred owls in the Eastern Cascade Mountains, Washington, USA, based on data collected from 2004 to 2006. The solid black line is the ratio for 95% kernel home ranges compared with the study area (second order), the bold gray line is the ratio for telemetry locations within home ranges compared with the 95% kernel home range (third order). Error bars show the 95% Bonferroni confidence interval for the ratio. Probability values indicate the probability of overall random use compared with availability across classes (Pearson's χ^2 statistic) for second (P_2) and third (P_3) order selection. Tick labels on the horizontal axis show the upper limit of the range of values for that class.

The resource-selection function we developed for barred owls in our study area indicated that the combination of topographic position, slope, NDVI, solar insolation, and an interaction term for canopy closure and tree crown diameter was the most effective for predicting relative probability of use (Tables 3, 4). The final model effectively distinguished between used and available areas (Figs. 4, 5).

DISCUSSION

Habitat Selection

Our findings that barred owls were associated with moist, structurally diverse, closed canopy forests on gentle slopes were consistent with patterns described in other barred owl studies from the Pacific Northwest (Herter and Hicks 2000, Gremel 2003, Pearson and Livezey 2003, Buchanan et al. 2004, Hamer et al. 2007). Home-range sizes during the breeding season in our study area were within the range of those reported for barred owls in other areas (Mazur et al. 1998, Mazur and James 2000, Harrold 2003, Livezey 2007). The home ranges we observed were smaller than those of barred owls in northwestern Washington, an area with relatively long winters and deep snowpack, which averaged 299 ha during summer and 950 ha during winter (95% adaptive kernel; Hamer et al. 2007).

Barred owls have been associated with structurally complex, closed-canopy forests across their range (Mazur and James 2000, Livezey 2007). The barred owls we studied avoided locating home ranges in areas with smaller trees and open canopy (tree crown diam <5.8 m and canopy closure <56%). Based on our field sampling to assess the accuracy of our vegetation maps, stands with the avoided tree crown diameter sizes had maximum tree diameter at breast height of <54 cm and had dominant trees smaller than 22–49 cm diameter at breast height (forest inventory and analysis size class 3; U.S. Forest Service 2005).

Several studies of barred owls in the Pacific Northwest have noted their association with moist bottomland forest (Herter and Hicks 2000, Gremel 2003, Pearson and Livezey

Table 3. The 5 models with the lowest Akaike's Information Criterion (AIC) values, and the intercept-only model, from the mixed-effect logistic regression analysis of 6 covariates for barred owl resource selection in the Eastern Cascade Range, Washington, USA, based on data collected from 2004 to 2006. Model covariates were topographic position (*tpos*), solar insolation (*solr*), slope (*slp*), canopy closure (*can*), overstory tree-crown diameter (*size*), and normalized difference vegetation index (*ndvi*). Interaction terms are indicated by a multiplication symbol (e.g., *can* × *size*); both main effects and interactions were included in all models with an interaction term. We included the individual owl as a random intercept effect in the mixed-effect logistic regression.

LL[a]	AIC	ΔAIC	K[a]	Formula
−1,615.2	3,248.4	0	22	$tpos + solr + slp + ndvi + (can \times size)$
−1,615.1	3,250.2	1.9	23	$tpos + solr + solr^2 + slp + ndvi + (can \times size)$
−1,629.1	3,274.1	25.9	21	$tpos + slp + solr + (can \times size)$
−1,629.1	3,376.1	27.7	22	$tpos + slp + solr + solr^2 + (can \times size)$
−1,631.2	3,278.3	29.9	21	$tpos + solr + slp + can + size + ndvi$
−2,187.6	4,379.1	1,130.8	15	intercept only

[a] LL = log likelihood; K = no. of parameters.

2003, Buchanan et al. 2004). Our finding that habitat use was associated with lower topographic position, gentle slopes, and high NDVI was consistent with that pattern. We found no strong association between habitat use by barred owls and proximity to water, with other studies reporting mixed results (Gremel 2003, Pearson and Livezey 2003, Buchannan et al. 2004, Hamer et al. 2007). Our impression was that habitat use was more strongly associated with highly productive moist forest than with open water. To our knowledge only one study in the Pacific Northwest investigated the distribution of sites inhabited by barred owl pairs in relation to aspect and found that aspect did not differ between spotted owls, barred owls, or random sites (Pearson and Livezey 2003). The association we found with habitat use by barred owls and moderate levels of solar insolation might be related to thermoregulation and prey availability, with sunnier areas providing warmer roosting sites during the nesting season and more moderate conditions during winter that may enhance prey populations (Lehmkuhl et al. 2006).

Interactions With Spotted Owls

The most striking ecological difference between barred owls and spotted owls in the Eastern Cascade Range is the difference in home-range sizes. Mean annual 100% MCP home range for 5 spotted owls on the Yakima Indian Reservation was 3,669 ha (SE = 876; King 1993), approximately 8 times larger than the mean annual 100% MCP home range for male barred owls that we documented. Annual 95% adaptive kernel home-range size for spotted owl pairs in the Cle Elum demography study area in central Washington ranged from 1,467 ha to 2,891 ha ($\bar{x}$ = 2,327 ha, n = 4 pairs; E. Forsman, United States Forest Service, Pacific Northwest Research Station, unpublished data), 4 to 9 times larger than the 332-ha annual pair 95% fixed-kernel home range we documented.

Sites inhabited by barred owl pairs in our study area were densely clustered in areas where important habitat characteristics were abundant, but sites overlapped little between adjacent pairs, which is consistent with the aggressive, territorial behavior widely reported for barred owls (Mazur and James 2000, Gutierrez et al. 2007, Livezey et al. 2007). Although we cannot assume that spotted owls were absent from areas we did not survey with spotted owl calls, it is worthwhile to note that the 2 sites where we confirmed presence and successful reproduction by spotted owl pairs were in the southern portion of the study area where our resource-selection function map showed that high-quality barred owl habitat was less abundant and relatively fragmented (Fig. 5).

Forest structural characteristics used by barred owls in our study were similar to those reported for spotted owls, which has been characterized as multispecies conifer forests dominated by large (>76-cm dbh) trees, moderate to high (60–80%) canopy closure, substantial structural diversity (including snags, down logs, mistletoe clumps, cavities, and broken tops), and canopy layering open enough to allow owls to fly within and beneath it (Thomas et al. 1990, Courtney et al. 2004, U.S. Fish and Wildlife Service 2008). Spotted owls in the Eastern Cascade Range have been found to use a slightly wider range of structural conditions than in the western portion of their range, particularly in areas where canopy structural complexity is enhanced by dwarf mistletoe (*Arceuthobium* spp.) brooms (King 1993, Everett et al. 1997, Irwin et al. 2004). Our finding that barred owls used forests with >70% canopy closure and crown diameter

Table 4. Coefficients for the best model of barred owl resource selection in the Eastern Cascade Range, Washington, USA, based on data collected from 2004 to 2006.

Covariate	Estimates	SE	z value	P
Mean intercept	−4.9030	0.7856	−6.24	<0.01
Topographic position	−0.0376	0.0027	−13.66	<0.01
Solar insolation (annual mean daily watt–hr/m^2)	0.0009	0.0001	6.89	<0.01
Slope (°)	−0.0486	0.0050	−9.72	<0.01
Canopy closure	−0.0145	0.0066	−2.21	0.03
Tree-crown diam (m)	−0.0009	0.0006	−1.44	0.15
Normalized difference vegetation index	0.0187	0.0036	5.18	<0.01
Canopy closure × tree-crown diam	0.00006	0.0001	5.72	<0.01

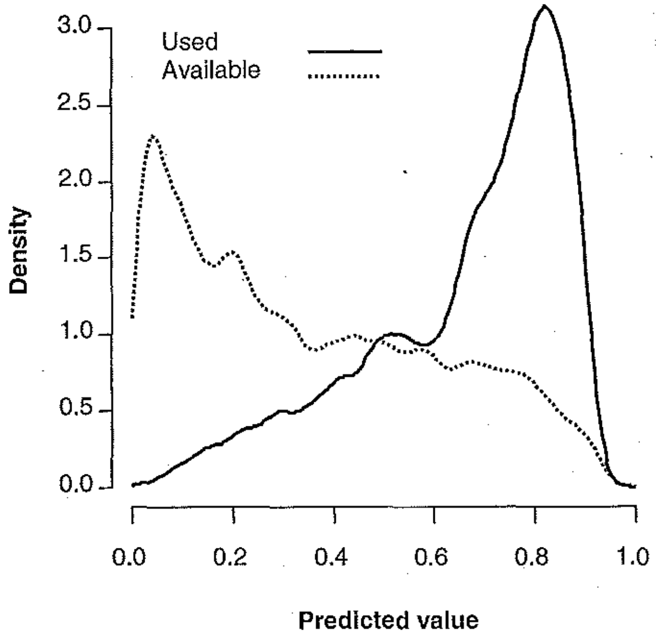

Figure 4. Density plot (bandwidth = 0.08) comparing predicted values from the resource-selection function at locations used by radiotagged barred owls in the Eastern Cascade Mountains, Washington, USA, based on data collected from 2004 to 2006 (used) to points drawn randomly from the study area (available). Predicted values were derived from the best logistic regression model of barred owl resource selection and calculated as *predicted value* $= e^z/(1 + e^z)$, where $z = [-4.093 - 0.0376 tpos + 0.0009 solr - 0.0486 slp - 0.0145 can - 0.0009 size + 0.0187 ndvi + 0.00006(can \times size)]$, *tpos* = topographic position, *solr* = solar radiation, *slp* = slope, *can* = canopy closure, *size* = overstory tree crown diameter, and *ndvi* = normalized difference vegetation index.

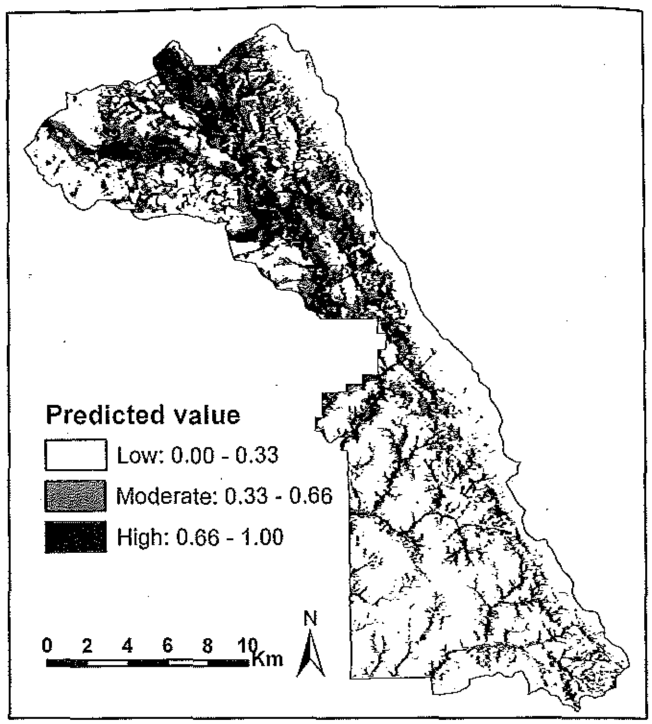

Figure 5. Relative probability of use by radiotagged barred owls in the Eastern Cascade Range, Washington, USA, derived from the best logistic regression model of resource selection based on data collected from 2004 to 2006.

>7.1 m (approx. 62-cm dbh max. tree size) more than other available forest, indicated that barred owls and spotted owls select sites with similar canopy closure and tree-size characteristics in our area.

Barred owls and spotted owls use forests with similar structural characteristics; however, barred owls in the Eastern Cascade Range appear to be more closely associated with moist forests on gentle slopes in valley bottoms. Several studies based on call survey results have reported that barred owls were located at lower elevations and on gentler slopes than spotted owls (Herter and Hicks 2000, Gremel 2003, Pearson and Livezey 2003). Buchanan et al. (2004) reported that 10 barred owl nests in the Eastern Cascade Range were located on gentler slopes, closer to water, and in areas with a wider variety of tree species than spotted owl nest sites, patterns consistent with our findings. In contrast, approximately 80% of 31 Eastern Cascade Range spotted owl neighborhoods (243 ha and 486 ha circles) were in Douglas-fir and grand fir plant associations classified as dry types (R. Schellhaas, United States Forest Service, Pacific Northwest Research Station, unpublished data). These differences in landscape use between barred owls and spotted owls may be related to differences in foraging ecology and prey selection (Hamer et al. 2001, 2007). Barred owls have small home ranges, centered on highly productive forest, and consume a wide variety of prey within that area (Livezey et al. 2007). Spotted owls use broader landscapes and specialize on larger-bodied arboreal prey (Bevis et al. 1997, Forsman et al. 2001, Hamer et al. 2007).

MANAGEMENT IMPLICATIONS

Differences in space use and habitat selection between barred owls and northern spotted owls may facilitate management that maintains forest characteristics appropriate for spotted owl habitat and prey in areas where spotted owls are least likely to be excluded by territorial barred owls in the Eastern Cascades of Washington. The structural diversity characteristic of spotted owl habitat in drier forests of the Eastern Cascade Range can be transient (Irwin et al. 2004). Managers will continue to be challenged by the conflicting objectives of maintaining that structural diversity while reducing the risk of loosing it during high-intensity wildfire or insect infestations (Lehmkuhl et al. 2007). Our findings that barred owl habitat use is concentrated in moist, valley-bottom forest often associated with fire refugia highlights this challenge (Camp et al. 1997, Pearson and Livezey 2007). Managers should be particularly cautious about extrapolating the results of this study beyond the Eastern Cascade Range of Washington. Differences in moisture gradients, forest productivity, and prey availability in other areas (particularly west of the Cascade Crest) may produce very different patterns than those we observed in the drier forests of the Eastern Cascades of Washington.

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